Reduced corticospinal responses in older compared to younger adults during submaximal isometric, shortening and lengthening contractions

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ABSTRACT

The aim of this study was to assess differences in motor performance, as well as corticospinal and spinal responses to transcranial magnetic and percutaneous nerve stimulation, respectively, during submaximal isometric, shortening and lengthening contractions between younger and older adults. Fifteen younger (26 ± 4 yrs, 7 females) and 14 older (64 ± 3 yrs, 5 females) adults performed isometric, and shortening and lengthening dorsiflexion on an isokinetic dynamometer ($5°\cdot s^{-1}$) at 25 and 50% of contraction type specific maximums. Motor evoked potentials (MEPs) and H-reflexes were recorded at anatomical zero. Maximal dorsiflexor torque was greater during lengthening compared to shortening and isometric contractions ($p<0.001$), but were not age-dependent ($p=0.158$). However, torque variability was greater in older compared to young ($p<0.001$). Background electromyographic (EMG) activity was greater in older compared to younger individuals ($p<0.005$) and was contraction type dependent ($p<0.001$). As evoked responses are influenced both by the maximal level of excitation and background EMG activity, the responses were additionally normalised ([MEP/M_{max}]/RMS and [H/M_{max}]/RMS). The (MEP/M_{max})/RMS and (H/Mmax)/RMS were similar across contraction types, but were greater in young compared to older adults ($p<0.001$). Peripheral motor conduction times were prolonged in older adults ($p=0.003$), whilst peripheral sensory conduction times and central motor conduction times were not age-dependent ($p\geq0.356$). These data suggest that age-related changes throughout the central nervous system serve to accommodate contraction type specific motor control. Moreover, a reduction in corticospinal responses and increased torque variability seem to occur without a significant reduction in maximal torque producing capacity during older age.

Key words: aging, concentric, corticospinal excitability, eccentric, H-reflex, motor evoked potentials, TMS

NEW & NOTEWORTHY

This is the first study to have explored corticospinal and spinal responses with aging during submaximal contractions of different types (isometric, shortening and lengthening) in lower limb musculature. It is demonstrated that despite preserved maximal torque production capacity, corticospinal responses are reduced in older compared to younger adults across contraction types along with increased torque variability during dynamic contractions. This suggests that the age-related corticospinal changes serve to accommodate contraction type specific motor control.

INTRODUCTION

The aging central nervous system (CNS) is characterised by physiological and functional decline (51, 77, 96) that can lead to an impaired ability to perform daily activities and a reduced quality of life. For example, older adults often exhibit a decline in maximal voluntary contraction (MVC) force. However, the degree of strength loss might vary across different muscle groups (23) and contraction type, with older adults typically displaying greater preservation of lengthening contraction strength (97). Additionally, even when older adults might not present a deficit in the generation of maximal force, underlying neural changes associated with aging could still be present (76). Force control appears to be a bigger challenge for the elderly during low (≤10% MVC) or higher (>50% MVC) intensity isometric contractions (38, 127) and during shortening and lengthening compared to isometric contractions (63, 64). Furthermore, older adults also exhibit a decline in force accuracy with particular tendency to exceed the target force during lengthening contractions (48). Whilst there are a number of age-related alterations within the muscular system (23), it has been postulated that the origin of performance variability with aging is due to CNS mechanisms (51).

Age-related alterations in the properties of motor units have received a great deal of attention in the literature (51, 77), whereas data on the modulation of corticospinal excitability with aging is comparatively understudied. The corticospinal pathway is the main descending pathway for control of voluntary movement (67), and can be non-invasively investigated using transcranial magnetic stimulation (TMS). The corticospinal responses could be impeded with aging due to the loss and/or atrophy of cortical neurons (44, 130) and reduction in white (72) and grey matter volume (75, 108), as well as instability of neuromuscular transmission (95). However, the indices of corticospinal excitability, such as the size of motor evoked potentials (MEPs) and the

slope of input-output relationship of TMS have been shown to be similar (42, 119, 122) or reduced (87, 94, 109) in older compared to young adults. These discrepancies have been suggested to be multifactorial (42), ranging from biological sex, contractile state (relaxed vs. active) and the muscle investigated (upper vs. lower limb).

The differences in corticospinal responses as a function of age have mainly been studied in upper limb muscles and might not translate well to lower limb, locomotor muscles due to differences in intracortical circuits and corticospinal projections (9, 12). With rare exceptions (e.g. 42), studies have not considered locomotor muscles. Furthermore, responses have largely been explored during rest or relatively low levels of muscle activity (e.g. 10% MVC; 42). Lastly, investigations have focused mainly on age-related changes in corticospinal excitability during isometric contractions. As highlighted recently, isometric actions are likely to be the least functionally relevant and thus assessment of the behaviour of the corticospinal output is required during dynamic contractions in an elderly population (77). Not solely relying on data examining corticospinal responses with aging in an isometric state is further supported by observations of reduced corticospinal and spinal responses during lengthening compared to isometric contractions in younger individuals (26–28, 39). Furthermore, given that the decrements in force control with aging are likely to be most prominent during dynamic contractions (10, 13, 63), it is important to elucidate whether the age-related changes in corticospinal responses are contraction-type dependent, in order to understand functional changes with aging.

It should be noted that any change in MEP size may be due to changes in the activity of cortical neurons or spinal motoneurons. Previously observed trends of reduced corticospinal excitability in older adults might, therefore, be related solely to altered activity of spinal motoneurons (122).

Notwithstanding its limitations (84), the Hoffmann (H) reflex has often been probed to investigate the spinal contribution to the overall response of the corticospinal pathway, however, in relation to aging this approach has only been applied during standing, i.e. isometric conditions (6), and not during dynamic contractions. Based on the age-related reduction in the H-reflex, but not maximal muscle response (M_{max}) latency, it has been postulated that the age-related decrease in conduction velocity and/or synaptic transmission efficacy is more prominent for sensory afferent axons compared to the efferent axons (111). However, further investigation is warranted, employing more robust measures, such as calculation of conduction times (128).

The purpose of this study was to assess the interplay between motor performance, the associated variability and differences in corticospinal and spinal responses during submaximal contractions of different types (isometric, shortening and lengthening) between younger and older adults. Tibialis anterior (TA) was targeted due to significant corticospinal drive during human locomotion (113) and association of poor motor performance of this muscle with a greater incidence of falls in the elderly (57, 131). We hypothesized that corticospinal (MEP amplitude) and spinal (H-reflex amplitude) responses will be reduced during dynamic contractions, conduction times of motor and sensory pathways will be prolonged and torque variability during dynamic contractions increased in older compared to young adults.

METHODS

Participants

A total of 29 participants took part in the experiment and were split into two groups, younger (n = 15, 7 females; 26 ± 4 years old, 175 ± 6 cm, 77.5 ± 12.8 kg) and older (n = 14, 5 females; 64 ± 3 years old, 173 ± 13 cm, 75.6 ± 16.1 kg). The lower limit of 60 years of age for the 'older' group was chosen based on the reported age-related changes in the neuromuscular system affecting motor function and performance (51). Prior to testing, participants responded to the questionnaire for contraindications for TMS (102) and a health screening questionnaire to ascertain contraindications to participation. The exclusion criteria for both groups of participants included any neurological or neuromuscular disorders, musculoskeletal injury that may attenuate the ability to produce torque, taking any medications known to affect the nervous system, and having pacemakers and intracranial plates. Participants were instructed to refrain from alcohol and strenuous exercise the day prior to testing and caffeine on the day of testing. To reduce the potential influence of female sex hormones on corticospinal excitability (120), premenopausal females not using hormonal contraceptives were tested in the luteal phase of the menstrual cycle. Females using a contraceptive pill were tested during the period of taking the oral contraceptive, thereby likely exhibiting a stable hormonal profile (30). The study conformed to the standards of Declaration of Helsinki. Participants eligible for the study gave written informed consent prior to any element of the study proceeding. All procedures were approved by Northumbria University Ethics Committee.

Study design

The study was designed to compare corticospinal and spinal excitability during submaximal isometric, shortening and lengthening dorsiflexion between young and older adults. Participants

visited the laboratory on 3 occasions, with a minimum of 48 h and a maximum of a week between sessions, at a similar time of day to limit diurnal variations (124). The three visits included: A) familiarization, B) assessment of corticospinal excitability, and C) assessment of spinal excitability. The order of the second and third visit was pseudorandomized and counterbalanced. The exact protocol depended on the type of experimental visit.

Procedures

Dynamometer setup and torque recordings

Participants were sat on an isokinetic dynamometer (Cybex Norm, Computer Sports Medicine Inc., Stoughton, MA, USA). All testing was performed on the dominant limb (15). Hip angle was positioned at 60° of flexion with the knee and the ankle at 90°. The foot was strapped securely to a metal plate attached to lever arm of the motor with a velcro strap. Particular attention was made to minimise extraneous toe movements. The distal part of the thigh was strapped down with velcro to minimise abduction, adduction and flexion of the hip. Furthermore, participants were instructed to focus solely on dorsiflexion and activation of TA. Visual feedback of the target torques was provided with the monitor placed approximately 1.5 m from the participant with the y-axis scale of visual display kept consistent for all contraction levels for all participants (−10 to 110% of participant's maximal voluntary contraction torque; MVC). For shortening and lengthening contractions, range-of-motion (ROM) was 10° of dorsiflexion and 10° of plantar flexion (total ROM of 20°, anatomical zero was taken when the ankle was at 90°). Contraction velocity for lengthening and shortening contractions was set at $5°\cdot s^{-1}$, giving a total contraction time of 4 s. Ten seconds before a shortening or lengthening contraction was performed, participants were passively moved into the starting position (10° of plantar flexion and 10° of dorsiflexion relative to anatomical zero for lengthening and shortening contraction, respectively) to minimize thixotropic effects (98). The dynamometer

was programmed to move the ankle once the participant had reached the target torque level in the starting position. Isometric contractions were performed with the ankle joint at anatomical zero and participants were instructed to increase the torque to an appropriate level and then maintain it for 4 s. Due to greater intrinsic force generating capacity of muscle fibres during lengthening contractions (29, 80), it was important to obtain contraction type specific MVCs (117). The greatest instantaneous torque was recorded for MVC during each contraction type and these values were used to standardise submaximal contractions at 25 and 50% of contraction type specific MVC that were performed in the experiment. During the experimental trials, participants were instructed to match the target torque line as closely as possible throughout the whole duration of the contraction.

Electromyography

Surface EMG was recorded by placing pairs of self-adhesive electrodes (8 mm diameter, 20 mm inter-electrode distance; Kendall 1041PTS, Tyco Healthcare Group, MA, USA) on the TA of the right limb according to the SENIAM recommendations (47) at one-third of the length between the tip of the fibula and the tip of the medial malleolus with the reference electrode placed over the patella. Additionally, to monitor antagonist muscle activity, electrodes were placed over the soleus at two-thirds of the line between the medial condyle of the femur to the medial malleolus. Prior to placement of electrodes, the recording site was shaved, abraded with preparation gel and wiped clean with an alcohol swab to ensure appropriate impedance (< 2 kΩ). The EMG signal was amplified (×1000), band pass filtered 20-2000 Hz (Neurolog System, Digitimer, Hertfordshire, UK) digitised (5 kHz; CED 1401, Cambridge Electronic Design, UK), acquired and analysed off line (Spike2, Cambridge Electronic Design, UK).

Percutaneous nerve and transcranial magnetic stimulation

Percutaneous stimulation of the peroneal nerve (PNS) below the head of the fibula, with a 1 ms pulse duration was performed using a 40 mm diameter cathode/anode arrangement (Digitimer DS7AH, Hertfordshire, UK). Responses were elicited during a weak contraction of 10% isometric MVC since H-reflex in TA is difficult to evoke at rest as reported previously (104). Upon localization of the optimal site, it was marked with a permanent marker and the stimulating electrode was strapped to participant's leg. The stimulation intensity was increased by 0.3 mA from H-reflex threshold every 3 pulses until the maximum M-wave (M_{max}) was reached. The current was then further increased by 30% to ensure supramaximal stimulation (current intensity: 54.4 ± 23.3 mA). Subsequently, M_{max} was elicited at 10, 25 and 50% of MVC, ensuring that the responses corresponded to the torque level at the point of stimulation. To minimise the potential for inducing fatigue, M_{max} was elicited only in the isometric state at different contraction levels since M_{max} has been shown to be dependent on position (35) and contraction intensity (66), but not on contraction type when elicited at the same joint angle (123). Similarly, the H-reflex was elicited at 10, 25 and 50% of MVC. The stimulus intensity used produced an M-wave amplitude of 15 – 20% of contraction level specific M_{max} (16). This ensured that the test H-reflex lied on the ascending limb of the input/output relationship of the motor neuron pool (60, 93).

A Magstim 200^2 stimulator (Magstim Co., Ltd., Whitland, UK; maximal output of ~1.4 T) with concave double-cone coil (110 mm diameter) was placed over the left primary motor cortex during contractions. Initially, the coil was positioned over the reported optimal spot for stimulation of the TA muscle, roughly 0.5-1 cm lateral and posterior to the vertex (20), and oriented to induce current in the posterior-to-anterior direction. The coil was then moved in small steps around the optimal until the position capable of evoking the biggest potential in TA (hotspot) was found. Once identified, the back of the coil was marked directly on the scalp with

229 a permanent marker to ensure consistent placement of the coil across the trials. After that, active
230 motor threshold (AMT) was determined during isometric contractions at 10% of MVC and was
231 defined as the lowest stimulator intensity to produce an MEP amplitude ≥ 200 μV in 3 out of 5
232 stimulations (58). As determining AMT at the contraction intensities employed in the
233 experiment (25 and 50% MVC) would have required a high number of contractions at both
234 intensities, we chose to select a lower contraction intensity to determine AMT in order to avoid
235 the occurrence of decrements in muscle functions as a result of performing multiple
236 contractions at higher intensities. Furthermore, standardising the intensity of stimulation at a
237 lower isometric contraction intensity allowed for investigation of MEP modulation with
238 increased contraction intensity, which has recently been shown to be similar regardless of
239 contraction type (118). During the experiment, TMS was standardised to 1.2 × AMT (stimulus
240 output: 39 ± 10%) as it lies on the middle portion of the ascending part of the stimulus-response
241 curve (41) and is thus sensitive to changes in corticospinal excitability.
242
243 As evoked responses are sensitive to changes in muscle length (35, 68), all forms of stimulation
244 were applied when the ankle joint was at, or passed through, anatomical zero (90°). To match
245 the timing of stimulation, during isometric contractions stimuli were delivered at the 2-second
246 point of a 4-second contraction. The consistency of timing and position of stimulations was
247 achieved using customised scripts (Spike2, CED, UK).
248
249 Experimental protocol
250 *A) familiarization*
251 During the initial visit, participants were familiarised with the contraction tasks and stimulation
252 techniques, i.e. PNS and TMS. This included receiving PNS at 10, 25 and 50% of isometric
253 MVC to determine M_{max}. Familiarisation with the contraction task involved a minimum of 10

contractions performed for each contraction type (isometric, shortening and lengthening) and intensity (25% and 50% of contraction-type specific MVC), since it has been suggested that no further within- or between-day improvements in torque variability are noted after 10 trials (48).

B) assessment of corticospinal excitability

Following a brief warm up involving individually estimated 50% submaximal isometric contractions, the session started with the determination of isometric MVC, followed by obtaining M_{max} at 25 and 50% of isometric MVC. Next, the TMS hotspot and AMT were determined whilst the participant maintained a contraction at 10% of isometric MVC. This was followed by the determination of shortening or lengthening MVC in a randomized order. Thereafter, participants performed isometric, shortening and lengthening contractions at 25 and 50% of contraction-type specific MVC in a randomised order and MEPs were recorded at each contraction type and intensity. Subsequently, the remaining contraction type was performed using the same protocol as described in the previous point. Four successful trials were recorded per contraction type and intensity and used for analysis. This number of trials was chosen as it has been shown to be the minimum required for adequate repeatability and validity of TMS (69), whilst also minimising fatigue and has been used previously in similar experiments (28). A trial was deemed successful if participants produced the target torque for 4 s and matched the target force level at the point of stimulation.

C) assessment of spinal excitability

The protocol for assessing spinal excitability replicated that of part B, but with replacement of TMS hotspot and AMT determination with determination of PNS stimulus intensity required to produce M-wave amplitude of 15-20% M_{max}. This stimulus intensity was then used for recording H-reflexes during the different contraction types and intensities. H-reflexes where the

M-wave did not meet the criterion stated above, were discarded. As per the criteria described above, four successful trials were recorded per contraction type and intensity and used for analysis, which ensured reliability and validity of PNS measures (82), has been used previously (28, 53), and minimised fatigue.

The levels of contraction intensity chosen allowed for comparison with other studies investigating corticospinal modulation during different contraction types (28, 39). Furthermore, only lower and medium contraction intensities, and not maximal, were studied since they have greater functional relevance (121) and are more likely to be difficult to control in older populations (48).

With regard to the chosen contraction velocity ($5°\cdot s^{-1}$), pilot testing indicated that higher contraction velocities led to significantly greater torque variability as shown previously (14), resulting in an inability to reliably deliver the stimuli at the desired torque output, particularly in an aging population. Since evoked responses are not only influenced by the stimulus intensity, but also the intensity of contraction (e.g. 117), higher contraction velocities could have led to differing relative torque levels across individuals, thus confounding comparability. Furthermore, a recent study showing differences in modulation of intracortical networks during shortening and lengthening contractions between young and older adults similarly employed a slow contraction velocity ($4°\cdot s^{-1}$; 89).

To minimize the decrements in muscle function due to repeated contractions, adequate rest was given where necessary. Following any MVC assessment, as well as between different contraction type sets, a minimum of 5 min rest occurred, whilst for different contraction levels within a contraction set at least 30 s was given. These rest periods have previously been shown to be sufficient to ensure that H-reflex (50) and MEPs (4) have returned to resting values. The duration of each session was roughly 1.5 h.

304

305 Fascicle length behaviour during shortening and lengthening contractions

306 To ensure that contraction types were distinct in the behaviour of contractile elements of the
307 muscle, measures of TA fascicle length were performed on a subsample of younger individuals
308 that were part of the original experiment (n = 8 (2 females): 27 ± 4 years old, 177 ± 7 cm, 79 ±
309 14 kg). During isometric, shortening and lengthening contractions ($5°\cdot s^{-1}$ for dynamic
310 contractions) at 50% of contraction-type specific MVC, ultrasound (AU5 Harmonic, Esatoe
311 Biomedica, Genoa, Italy) images of the TA fascicles were record in real-time, sampled at 25
312 Hz (AVer Media Capture Studio, AVer Media Technologies, New Taipei City, Taiwan). Only
313 one contraction intensity was investigated since the rate of change in fascicle length has been
314 shown to be similar during shortening and lengthening contractions in TA across a range of
315 contraction intensities (91). After identification and marking of the proximal and distal insertion
316 of the muscle, a B-mode linear array probe (7.5 MHz, 55 mm width) was held with a constant
317 light pressure, perpendicular to the dermal surface along the midsagittal plane of the TA. The
318 probe was positioned at the site corresponding to the thickest portion of the muscle as identified
319 by the ultrasound (8, 100). An echo-absorptive marker was placed between the skin and the
320 probe to ensure there was no movement artefact included in the assessment of fascicle length.
321 A hypo-allergenic ultrasound gel (Parker, Park Laboratories Inc., Fairfield) was used to enhance
322 coupling between the skin and the probe. An externally generated square wave pulse was used
323 to synchronise the ultrasound images with the dynamometer position acquisition system.
324 Frame-capture software (Adobe Premier Elements, version 15) was used to acquire ultrasound
325 images (frame corresponding to every degree of ankle angle) for offline analysis (ImageJ 1.45,
326 National Institutes of Health, USA). Fascicle length was measured from central to the
327 superficial aponeurosis of TA (100). The fascicle was measured if it remained visible across
328 the entire ultrasound image. Where the fascicle extended beyond the ultrasound image, linear

continuation of the fascicle and aponeurosis was assumed (3, 100). To reduce error associated with estimation of fascicle length, an average of three fascicles across the image was taken (40). Fascicles were analysed every 5˚ of ankle angle throughout the 20˚ range-of-motion during shortening and lengthening contractions, and every second during isometric contractions corresponding to the timing of every 5º-change during dynamic contractions.

Data Analysis

Torque and root-mean-square background EMG activity (RMS EMG) were assessed in the 100-ms epoch preceding the stimulus. RMS EMG of TA was normalised to M_{max} (RMS/M_{max}) in order to remove the confounding effect of electrode location and body fat (65), and account for changes at the skin-electrode interface and differences in propagation along the sarcolemma (83). Torque variability during submaximal contractions was assessed as coefficient of variation (CV_{torque} = SD torque /mean torque*100) in the 1-second epoch preceding the stimulus. The analysed time-frame ensured that the acceleration phase at the start of the movement was not included in the analysis. Peak-to-peak amplitudes of MEPs were calculated and were normalized to the peak-to-peak amplitude of M_{max} obtained during the same contraction intensity (MEP/M_{max}). Peak-to-peak amplitudes of M_{max} and H-reflex were calculated and were subsequently normalized to peak-to-peak amplitude of M_{max} obtained during the same contraction intensity (H/M_{max}). Additionally, peak-to-peak amplitude of the M-wave evoked with an H-reflex (M_H) was calculated and normalized to peak-to-peak amplitude of M_{max} obtained during the same contraction intensity (M_H/M_{max}) to ensure the same proportion of motor units were activated across all trials (26). MEP, H-reflex and M_{max} latencies were calculated from stimulus artefact to initial deflections of the TA EMG from baseline. All latencies were measured from individual trials and subsequently averaged. Peripheral motor conduction time (PMCT) was estimated using the F-wave and M-wave obtained at 50% of

isometric MVC using the standard equation: (F latency + M latency – 1)/2. To estimate central motor conduction time (CMCT), PMCT and 0.5 ms (to account for synaptic delay between corticospinal axons and alpha motoneurons) were subtracted from the MEP latency obtained during 50% of isometric MVC. Peripheral sensory conduction time (PSCT) was also estimated at 50% isometric MVC using the equation H-reflex latency – PMCT – 0.5 ms. Since conduction time to lower limbs is confounded by differences in height (34, 128), PMCT, CMCT and PSCT values were additionally normalised to participant height.

Statistical analyses

All analyses were performed using SPSS package (v20, SPSS Inc., Chicago, IL, USA). Statistical significance was set at an alpha level of 0.05. Normality was assessed using Shapiro-Wilks test. If the data were not normal, transformations were performed using common logarithm for positively skewed data. A 2-way mixed-effect intraclass correlation coefficient ($ICC_{3,1}$) model for absolute agreement (115) and coefficient of variation (CV) were used to assess between-day reliability and variability, respectively, of maximal torque and M_{max}. An ICC $\geq$ 0.9 was considered excellent reliability, and an ICC of 0.75-0.9 was classified as good reliability (61). A one-sample T-test was used to assess the differences between the actual and target torque at the point of stimulation. An independent samples T-test was used to assess differences in peripheral and central motor conduction time between young and older adults. Association between torque variability and corticospinal and spinal responses was assessed using Spearman's correlation coefficient. Sphericity was assessed using Mauchly's test of sphericity. In the case of violation, a Greenhouse-Geisser correction was employed. A two-way mixed ANOVA with repeated measures design was used to investigate the differences in fascicle length during shortening and lengthening contractions with ankle joint movement. A

379 one-way repeated measures ANOVA was used to investigate the differences in fascicle length
380 across contraction types at anatomical zero and the potential differences in fascicles length
381 during 4-second isometric contractions. A three-way mixed ANOVA with repeated measures
382 design was employed to analyse differences in corticospinal and spinal responses, EMG activity
383 and CV_{torque} between contraction types, contraction intensity and age group. An additional
384 factor of 'visit' was added to ANOVA to explore differences in MVC and M_{max} across different
385 testing days. When significant F-values were found, the post hoc pairwise comparison was
386 performed with a Bonferroni correction for multiple comparisons. In some cases where the F-
387 values and p-values were similar on both days, the minimum and maximum, respectively, are
388 reported. Data are presented as mean ± SD, unless the data had to be transformed, in which case
389 the geometric mean ± SD are presented.

RESULTS

Fascicle length changes

Fascicles did not vary in length during isometric contractions ($F_{2.3, 16.0} = 2.7$, $p = 0.090$; Figure 1). However, fascicle length changed linearly with changes in joint angle during shortening and lengthening contractions ($F_{1.3, 9.1} = 94.2$, $p < 0.001$), with no differences in the slope of fascicle length changes between contraction types ($F_{4, 28} = 2.2$, $p = 0.091$). Fascicle length decreased by 36% during shortening contractions (from 48.1 ± 3.8 to 35.2 ± 3.9 mm) and increased by 34% during lengthening contractions (from 35.4 ± 3.5 mm to 47.4 ± 3.0; Figure 1). At anatomical zero, where stimulations were subsequently performed, fascicle length was similar during isometric (41.1 ± 3.9 mm), shortening (40.3 ± 3.7 mm) and lengthening (41.1 ± 3.6 mm) contractions ($F_{2, 14} = 1.3$, $p = 0.292$).

Maximal torque and M_{max}

Maximal voluntary torque did not differ between the visits ($F_{1.6, 43.1} = 1.6$, $p = 0.213$) and a good to excellent between-day repeatability (ICCs > 0.8) and low variability (CV < 10%) was established for MVCs (Table 1). MVC was contraction type dependent ($F_{1.3, 35.4} = 139.3$, $p < 0.001$) such that isometric and shortening maximal torque were ~24% lower compared to lengthening ($p < 0.001$ for both age groups; Figure 2A and B), with no differences between age groups ($p = 0.158$).

Similarly, M_{max} was not different across visits ($F_{2, 54} = 3.3$, $p = 0.089$), and displayed good to excellent repeatability (ICCs > 0.8) and low variability (CV < 15%; Table 1). M_{max} amplitude was contraction intensity dependent ($F_{1.3, 36.3} = 38.6$, $p < 0.001$) such that it increased ~5-8% with greater contraction intensity ($p < 0.001$ for all cases; Figure 2C and 2D). Whilst a main effect of contraction intensity was found for M_{max} latency ($F_{1.7, 44.6} = 4.1$, $p = 0.031$), pairwise comparison with Bonferroni correction did not reveal any other differences (Figure 2E and 2F).

PMCT was prolonged in older (11.4 ± 0.7 $ms \cdot m^{-1}$) compared to younger (10.6 ± 0.6 $ms \cdot m^{-1}$) adults ($t_{27} = -3.2$, $p = 0.003$).

Torque variability during submaximal contractions

CV_{torque} was dependent on contraction type ($F_{2, 54} > 246$, $p < 0.001$) and age ($F_{1, 27} > 23$, $p < 0.001$) and there was a significant contraction type × age interaction ($F_{2, 54} > 5$, $p < 0.007$). Older compared to young individuals had greater CV_{torque} during shortening and lengthening contractions ($p < 0.001$ for both; Table 2). In older adults, CV_{torque} was ~5-fold greater during shortening compared to isometric ($p < 0.001$) and ~1.5-fold compared to lengthening ($p = 0.001$), as well as ~3.5-fold greater during lengthening compared to isometric contractions ($p < 0.001$). In young individuals however, CV_{torque} was ~3-fold greater during shortening and lengthening compared to isometric contractions ($p < 0.001$ for both). No association was shown between CV_{torque} and any responses to stimulation techniques (p value range = 0.067 – 0.223, r = 0.499 – 0.600).

Torque at stimulation and voluntary background EMG

On average, participants matched the target torque level at the point of stimulation during isometric and shortening contractions, but had a tendency to overshoot the target torque during lengthening contractions (Table 2).

The RMS/M_{max} during both experimental visits increased with contraction intensity ($F_{1, 27} > 166$, $p < 0.001$) and age ($F_{1, 27} > 11$, $p < 0.005$), and was modulated with contraction type ($F_{2, 54} > 14$, $p < 0.001$). Significant contraction type × age ($F_{2, 54} > 4$, $p < 0.001$) and contraction intensity × age interactions ($F_{2, 54} > 11$, $p < 0.005$) were noted. *Post hoc* testing revealed that in young individuals greater RMS/M_{max} was displayed during shortening compared to isometric ($p < 0.001$) and lengthening ($p < 0.015$) contraction, whilst in older individuals greater

440 RMS/M_{max} was observed during shortening ($p < 0.001$) and lengthening ($p = 0.003$) compared
441 to isometric contractions (Table 2).
442 The RMS activity of soleus during both experimental visits increased with contraction intensity
443 ($F_{1,27} > 20$, $p < 0.001$) and was dependent on contraction type ($F_{2,54} > 16$, $p < 0.001$), but not on
444 age ($F_{1,27} > 0.2$, $p > 0.387$). There was a significant contraction type × age interaction ($F_{2,54} >$
445 7, $p < 0.005$). In younger individuals antagonist RMS activity was greater during shortening
446 compared to isometric contractions ($p = 0.001$), whilst in older individuals, antagonist RMS
447 activity was greater during shortening ($p = 0.004$) and lengthening ($p < 0.001$) contractions
448 compared to isometric (Table 2).
449
450 *Responses to PNS*
451 Representative examples of responses to PNS for a young and an older individual of similar
452 height during 25% of contraction type specific MVC are presented in Figure 3A. Notably, it is
453 clear that the older individual in these plots exhibited smaller H-reflexes as well as slightly
454 longer latencies and this trend was similar during all contraction types at both contraction
455 intensities.
456
457 M_H/M_{max} was similar across all conditions ($p \geq 0.116$; Table 2). H/M_{max} increased with
458 contraction intensity ($F_{1, 27} = 58.4$, $p < 0.001$), was greater in younger adults compared to older
459 ($F_{1, 27} = 6.0$, $p = 0.021$) and was contraction type dependent ($F_{2, 54} = 16.2$, $p < 0.001$). There was
460 a contraction type × contraction intensity × age group interaction for H/M_{max} ($F_{2, 54} = 6.6$, $p =$
461 0.003). *Post hoc* analysis showed younger individuals had ~38% greater H/M_{max} compared to
462 older during lengthening contractions at 25% of maximal torque ($p = 0.004$; Figure 3B & C),
463 as well as ~33% during isometric ($p = 0.020$) and shortening ($p = 0.008$) contractions at 50%
464 of maximal torque (Figure 3D & E). Furthermore, in younger individuals, H/M_{max} was ~43%

greater during shortening compared to isometric contractions at 25% ($p = 0.001$; Figure 3B) and ~43% greater compared to lengthening contractions at 50% of maximal torque ($p = 0.010$; Figure 3D). Older individuals exhibited ~43% greater H/M_{max} during shortening compared to isometric ($p = 0.007$) and lengthening contractions ($p < 0.001$) at 25% of maximal torque (Figure 3C), but no differences were noted across contraction types at 50% of maximal torque ($p > 0.05$). H/M_{max} increased ~71% with contraction intensity in young adults during isometric ($p < 0.001$) and ~43% compared to shortening ($p = 0.001$), but not lengthening contractions ($p = 0.059$). In older adults, H/M_{max} increased ~43% with contraction intensity during isometric ($p = 0.004$) and ~25% compared to lengthening ($p < 0.001$) contractions, but not shortening ($p = 0.063$).

H-reflex latency was similar across contraction intensities and types ($p > 0.05$). Whilst the mean group values suggested H-reflex latencies were longer in the older population (Table 2), this difference did not reach statistical significance ($F_{1, 27} = 3.9$, $p = 0.058$). PSCT was similar between young and older individuals (8.1 ± 0.9 vs. 8.5 ± 2.0 ms.m^{-1}; $t_{27} = -0.5$, $p = 0.473$).

Responses to TMS

Example responses to TMS for representative participants of similar height during 25% of contraction type specific MVC are presented in Figure 4A. As noted by the dashed lines in the figure, older individuals exhibited longer MEP latencies and smaller amplitude of responses compared to younger individuals. Similar behaviour was observed during contractions at 50% of maximal torque.

MEP/M_{max} increased ~34% with greater contraction intensity ($F_{1, 27} = 43.7$, $p < 0.001$) and was contraction type dependent ($F_{2, 54} = 14.1$, $p < 0.001$). No differences were observed between groups ($p = 0.290$). There was a contraction type × age group interaction ($F_{2, 54} = 3.5$, $p = 0.039$).

Post hoc testing show that in young individuals MEP/M_{max} was ~23% greater during shortening compared to lengthening ($p = 0.002$) contractions (Figure 4B & D). However, in older adults, MEP/M_{max} was ~43% greater during shortening ($p = 0.001$) and ~24% greater during lengthening ($p = 0.024$) compared to isometric contractions (Figure 4C & E).

Older individuals exhibited ~15% longer MEP latencies compared to young ($F_{1, 27} = 5.6$, $p = 0.025$; Table 2). As per significant interaction between contraction type and age group ($F_{2, 54} = 4.5$, $p = 0.015$), the magnitude of this difference was greater during lengthening contraction ($p = 0.006$). However, CMCT was not different between young and older adults (6.2 ± 2.1 vs. 6.9 ± 1.9 $ms \cdot m^{-1}$; $t_{27} = –0.9$, $p = 0.350$).

The influence of background activity on the evoked responses

Modulation of responses to stimulation techniques during submaximal contractions may not just depend on torque, but also on background EMG activity (1, 39, 86). Whilst care was taken to record responses at the same relative torque levels for each contraction type (117) with stimulation performed at the same joint angle in all conditions, differences in RMS/M_{max} between contraction types and age groups were still observed. Thus, the evoked responses to stimulations were additionally normalised to the pre-stimulus RMS activity ([H/M_{max}]/RMS and [MEP/M_{max}]/RMS, respectively), as has been done previously (116, 123). The [H/M_{max}]/RMS did not change with contraction type ($F_{2, 54} = 4.6$, $p = 0.275$), but was greater in younger individuals ($F_{1, 27} = 19.8$, $p < 0.001$), and was modulated with contraction intensity ($F_{1, 27} = 7.6$, $p = 0.010$). There was a contraction intensity × contraction type × age interaction ($F_{2, 54} = 7.4$, $p = 0.001$). *Post hoc* analysis showed older individuals exhibited ~33% smaller [H/M_{max}]/RMS during lengthening compared to isometric ($p = 0.034$) and shortening ($p = 0.020$) contraction at 25% of maximal torque (Figure 5A). Furthermore, older compared to

younger individuals exhibited ~44% smaller [H/M_{max}]/RMS across all contraction types and intensities ($p < 0.028$; Figure 5A-D).

Similarly, [MEP/M_{max}]/RMS was not dependent on contraction type ($F_{2, 54} = 1.5$, $p = 0.236$); however, it was ~34% lower in older individuals ($F_{1, 27} = 15.7$, $p < 0.001$; Figure 5E–H) and modulated with contraction intensity ($F_{1, 27} = 11.4$, $p = 0.002$). A significant interaction between contraction intensity and age ($F_{1, 27} = 4.8$, $p = 0.037$) showed that the difference in [MEP/M_{max}]/RMS with contraction intensity was only significant for younger individuals ($p < 0.001$).

DISCUSSION

The present study investigated corticospinal and spinal responses in relation to motor performance variability in younger and older individuals. The novel findings of the present study are the manifestation of corticospinal and spinal changes along with increased torque variability without decrements in maximal torque production in older adults. Specifically, peripheral motor conduction times were longer, the amplitudes of MEP and H-reflexes when accounting for differences in background EMG activity were smaller, and CV_{torque} was greater in older compared to younger adults during shortening and lengthening contractions.

Maximal torque production and torque variability

Older adults were of similar strength compared to young counterparts, but their motor performance during submaximal contractions was poorer. Whilst healthy aging has been associated with the decline in peak torque production (37, 76, 92), this might not always be the case, particularly in the dorsiflexors (59, 62), a muscle group with similar habitual use in older age and thus, better preserved function (2, 90). It has also been argued previously that changes in motor performance are less accurate in older adults due to greater within- and between-subject variability in performance (18, 99), rendering the age-related changes in motor performance measures less detectable (51). The lack of statistical age-difference in the present study could thus be due to greater between-subject heterogeneity of older adults during MVC (see SDs in Table 1). This greater heterogeneity of older adults compared to the young was evident during isometric and shortening contractions, whereas it was similar during lengthening contractions, which might stem from greater preservation of strength during lengthening contraction in older adults (97). Alternatively, the average age of participants in the older group might have been too low for differences in MVC to be detected. However, the lack of dorsiflexor strength difference between young and older adults has previously been observed

547 even when participants were over 70 years of age (59, 62). Since the loss of voluntary strength
548 with aging seems to be related to the degree of sarcopenia (36, 79, 92), it seems more likely that
549 at least some of our older individuals were pre-sarcopenic, rather than not sufficiently old per
550 se. Another factor that could have contributed to the lack of age-related difference in MVC is
551 uneven distribution of sexes between the young and the older sample, as the rate of age-related
552 strength decline appears to be greater for males than females (21, 132).
553 Despite the lack of difference in MVC, older individuals displayed greater variability of torque
554 output during submaximal shortening and lengthening contractions as well as a tendency to
555 overshoot the target torque. The lack of relationship between maximal strength and torque
556 variability during submaximal contractions has previously been demonstrated in older adults
557 (10), as well as greater torque variability during dynamic contractions (63) and the tendency to
558 overshoot the target torque (48). This greater variability and reduced accuracy in matching the
559 target torque is likely responsible for higher background EMG activity in older adults, a finding
560 consistent with previous literature, especially during fine motor tasks (56, 89). Alternatively,
561 the greater agonist EMG activity could stem from differences in antagonist EMG activity.
562 Whilst our data does not demonstrate any age-group differences in antagonist EMG activity,
563 potential differences could be masked by the lack of normalisation to the maximal EMG activity
564 of the antagonist.
565
566 *Differences in responses to stimulations as a function of age*
567 M_{max} amplitude was not different between younger and older adults, but M_{max} increased with
568 greater contraction intensity independent of age as shown previously (66). No difference in
569 MEP amplitude was observed between younger and older individuals during a constant torque
570 task across contraction types. However, when the difference in background EMG activity
571 between the age groups was accounted for, younger individuals displayed greater corticospinal

responses compared to older regardless of contraction type, as shown previously (87, 109). The greater EMG activity, but a lack of difference in MEP/M_{max} at the same relative submaximal target torque might suggest a compensatory increase in corticospinal drive in older adults for maintenance of the desired torque level when compared to younger adults (114). Interestingly, the representative responses in Figure 4A show a polyphasic waveform as shown previously in TA (126), and a slightly differing waveform shape between young and older individuals which might stem from differences in I-wave recruitment (88). However, further investigation of this behaviour is beyond the scope of this study. Reduced corticospinal responsiveness with advancing age observed in the present study might occur due to various factors, including decreased quantity of cortical neurons and their functionality (44, 114). However, MEP size depends on excitability of both cortical neurons and spinal motoneurons and hence the differences between younger and older adults could stem from alterations in either or both of these neural axes.

H-reflex is generally considered to be a measure of spinal excitability and can be influenced by the level of alpha motoneuron excitability, presynaptic inhibition (11, 112), spinal interneuronal activity (84, 101) and supraspinal centres (43, 106). The level of alpha motoneuron excitability can be linked to Ia synaptic input and hence a lower H-reflex seen in older individuals could suggest a loss of Ia axons and their synaptic input. However, in the present study this seems unlikely as the PSCT values for the older group would have been expected to have been greater in comparison to the young, which was not the case. The lower H-reflex (H/M ratio) in older individuals is consistent with an increased presynaptic inhibition in this group as previously reported (53, 81, 107, 111). It is of interest that the greater EMG activity of the agonist observed in older adults was insufficient to compensate for the increase in presynaptic inhibition. This would suggest other changes in spinal excitability might be occurring. For instance, recent

animal work has shown that aging is associated with reduced facilitatory glutamatergic inputs to the spinal cord (74), which could reduce motoneuronal output. Whilst this notion would suggest that the change in MEP size is more likely due to age-related alterations in the activity of the spinal motoneurons rather than cortical neurons, it should be noted that H-reflex is influenced by presynaptic inhibition, whereas MEP amplitude is not (85). Thus, future work involving electrical stimulation of descending pathways at a subcortical level (125) is warranted to provide more definite conclusions.

MEP latencies were longer in older individuals, a finding previously observed in an elderly population, which might stem from age-related alterations in temporal characteristics of interneuronal (I-wave) circuitry (88). Whilst H-reflex latencies were not statistically different between groups (mean difference: 2.0 ms; $p = 0.058$), there was a trend for longer latencies in older adults, which has been previously demonstrated (59, 107, 111). Prolonged H-reflex latency along with no difference in M_{max} latency would suggest that sensory afferent axons were more affected with aging than efferent motor axons, as previous studies have also suggested (110). However, such a conclusion does not take into account the shortness of the motor pathway, and consequent shorter latency for M_{max}, making it difficult for any differences in M_{max} latency to be detected. For instance, M_{max} latency increased by the same percentage as H-reflex latency (~6%), however an absolute increase of ~0.3 ms is likely too small to be detectable. Despite no statistical difference in M_{max} latency, the difference in PMCT between young and older adults, combined with no difference in PSCT and CMCT suggests that it is the efferent motor axons that are more affected by aging. This could stem from the loss of large-diameter axons (54, 55) as well as reductions in myelination and internodal length (24, 78) associated with advancing age. Collectively, the age-related differences in MEP and H-reflex

amplitudes and conduction times suggest that changes occurring in CNS could be more prominent at the spinal and motoneuronal, rather than cortical level.

Relationship between functional and corticospinal changes with aging

The interesting finding in the present study is the interplay between corticospinal changes and functional alterations in older adults as they exhibited reduced corticospinal and spinal responses compared to the young, but showed divergent functional adjustments. The prolonged PMCT in older adults is suggestive of the loss of large-diameter motor axons (54, 55). The loss of such axons could lead to sprouting of surviving alpha-motoneuron axons to reinnervate the denervated muscle fibres (19, 45, 71), thus facilitating maintenance of maximal torque production. However, reinnervation leads to large motor units resulting in larger and more variable motor unit action potentials (49), which might contribute to increased torque variability during submaximal contractions. However, despite the plausibility of the aforementioned notion, further research is needed to test this hypothesis directly. The probability of older adults having enlarged motor units, but preserved maximal torque production in the present study suggests that they were mostly pre-sarcopenic (36, 92). Whilst it has been shown previously that neural changes, such as alterations in motor unit properties, can precede the loss of maximal torque production with aging, especially in pre-sarcopenic older adults (36, 76, 92), the present study extends this observation by showing there is also a decline in corticospinal and spinal responses that might occur in advance of substantial age-related maximal torque losses. Despite the preserved capacity to generate maximal torque, age-related functional alterations can still be manifested, as evidenced by increased torque variability. The latter is likely to impact activities of daily living to a greater extent than losses in maximal strength since most of the activities of daily living are submaximal, requiring fine motor control. Thus, the assessment of

age-related loss in function requires an investigation of multiple variables, rather than solely relying on measures of MVC.

Whilst older adults demonstrated reduced corticospinal and spinal responses concurrent with increased torque variability compared with young adults, no association was shown between corticospinal and/or spinal responses and torque variability. A previous study demonstrated a lack of relationship between motor performance variability and intracortical inhibitory activity (89), and the present study extends this observation by suggesting a reduction in corticospinal and spinal responses in older age are not related to reductions in motor performance variability during submaximal shortening and lengthening contractions. As previously outlined, there is a possibility that a lack of relation between corticospinal responsiveness and torque variability is due to improvements in motor performance after sufficient familiarisation and repeated performance of the task throughout the experiments (89) despite no observation of a systematic improvement in task performance in both experimental sessions. Alternatively, though corticospinal excitability might contribute to the common synaptic input to a greater or lesser extent depending on age, it is likely the modulation of that common input that directly determines the variability of torque output (32).

Corticospinal and spinal modulation during isometric, shortening and lengthening contractions

Lengthening contractions have been purported to be accompanied by reduced corticospinal responses (for review see 25). However, when background EMG activity was accounted for in the present study, MEPs and H-reflexes were not differently modulated across isometric, shortening and lengthening contractions. The MEP behaviour corroborates a study on soleus when comparing their responses elicited with similar relative TMS intensity to the present study (28). Conversely, the lack of H-reflex modulation observed in the present experiment does not

support reduced spinal excitability during lengthening contractions previously reported in soleus (28, 101). This discrepancy could be the result of differences in tasks employed between experiments (constant torque versus 'constant length'; 28, 116), slower contraction velocity (101), differences in EMG activity between contraction types (28), and differences in joint angles and the corresponding muscle length between TA and SOL (22, 46). Furthermore, the familiarisation sessions involving submaximal lengthening contractions could have led to motoneuron pool adjustments as a strategy to protect the muscle from damage (17, 52), thus potentially affecting evoked responses in the experimental session. Despite aforementioned confounding methodological factors, it is important to consider that the H-reflex behaviour might be muscle-specific. Indeed, similarly to data in the present study, no H-reflex modulation across contraction types has previously been shown for medial gastrocnemius (27). From the perspective of spinal control, TA and SOL are known to differ in quantity of muscle spindles (~280 versus ~400; 5, 70) and the strength of reciprocal spindle afferent input (4-fold greater in TA; 132), both of which could affect the relative input from Ia afferents. Thus, it is possible that the observed behaviour in TA in the present study is specific to the muscle investigated.

Methodological considerations

The aim of this study was not only to assess corticospinal and spinal excitability during submaximal isometric, shortening and lengthening contractions with advancing age, but also to concurrently explore functional measures of torque variability. As such, the submaximal contraction targets were based relative to an individual's maximal torque production capacity. Despite normalising to contraction type specific MVC (117), this approach resulted in differing background EMG activity levels across contraction types and between young and older adults. The evoked response size is known to increase concurrently with background EMG activity (31, 33, 103) due to greater motoneuron excitability as a result of motoneurons being closer to

their firing threshold with augmentation of their recruitment and firing rate (7). The size of MEPs is increased with greater background EMG activity even when normalised to contraction intensity specific M_{max} (73). As such, the differences in background EMG across conditions could have confounded our interpretation of the differences in the evoked responses across contraction types and between the age groups. To account for this possibility, corticospinal and spinal responses were additionally normalised to background EMG activity as seen previously (116, 123). However, furture work is required to elucidate whether behaviour observed in this study is similar when the level of neural excitation is matched across conditions.

The contraction velocity chosen ($5°\cdot s^{-1}$) could be considered slow. This is a potential reason for the lack of difference observed in maximal torque production between isometric and shortening contractions (105) as well as differences between age groups across contraction types (97, 105). Furthermore, the slower velocity might have made it less likely that neural strategies during dynamic contractions will differ from isometric. The reason for the selection of this velocity was based on pilot testing that indicated difficulty in reliable delivery of stimuli during submaximal contractions at the target torque due to significant torque variability with increased contraction velocity. Moreover, the contraction velocity chosen allowed for a sufficient pre-stimulus time of torque production for a reliable analysis of torque variability. However, our data showed orthodoxical shortening and lengthening of muscle fascicles with changes in joint angle during dynamic contractions, whereas fascicles exhibited no change in length during isometric contractions, suggesting the behaviour of contractile elements during different contraction types was indeed distinct. Fascicles were also of analogous length at the anatomical zero, confirming responses were elicited at the same muscle length. Moreover, a recent study indicated that corticospinal and spinal responses during lengthening contractions do not change with a 4-fold increase in contraction velocity (129), suggesting that an increase in proprioceptive feedback with increases in contraction velocity does not seem to influence the

potential differences in corticospinal control of different contraction types. Nevertheless, future studies are required to investigate velocity-dependence of the corticospinal responses observed in the present study, particularly at very fast velocities, and since maximal strength during dynamic contractions in older adults seems to vary with velocity (97).

Conclusion

The present study showed that despite no difference in maximal torque production, corticospinal and spinal excitability were greater and peripheral motor conduction time was shorter in young compared to older adults. These findings suggest that corticospinal changes associated with aging can occur in advance of decrements in maximal torque production in TA, whereas other functional alterations, such as increased torque variability and reduced torque accuracy during submaximal dynamic contractions, are still evident. More work is needed to determine the timeline of interaction between neural and different functional alterations associated with healthy aging. Interestingly, the present data show the pattern of corticospinal modulation of different contraction types between younger and older adults during a constant torque task in dorsiflexors is similar. This suggests that the CNS accommodates for age-related changes in order to preserve motor control of different contraction types. Additionally, the results show that in a constant torque task, corticospinal and spinal excitability of dorsiflexors are greater during shortening compared to isometric and lengthening contractions, but no differences are apparent when variances in background EMG activity are taken into account. These responses do not support the notion of a unique corticospinal control of lengthening dorsiflexion and might be task (i.e. a constant torque task) or muscle-specific (i.e. TA). Further investigation is required to elucidate whether similar behaviour between young and older adults is observed during actions of the other muscles across different tasks, similar background levels

744 of activation, contraction intensities and velocities as well as delivery of stimuli at different
745 muscle lengths.
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Table 1. Maximal voluntary torque and maximal muscle response (mean ± SD), between-day repeatability ($ICC_{3,1}$ with 95% confidence intervals) and variability (coefficient of variation – CV%) across the three visits (familiarisation, TMS and PNS).

			ALL	YOUNG	OLDER
MVC Torque (N·m)	Isometric	Familiarisation	40.9 ± 9.9	43.3 ± 7.8	38.4 ± 11.5
		TMS	42.1 ± 10.8	46.0 ± 10.1	38.7 ± 12.5
		PNS	41.8 ± 11.7	45.4 ± 8.1	37.4 ± 11.9
		$ICC_{3,1}$ (95% CI)	0.90 (0.82 - 0.95)	0.77 (0.55 - 0.91)	0.96 (0.91 - 0.99)
		CV (%)	6.8 ± 4.6	7.8 ± 4.8	5.6 ± 4.2
	Shortening	Familiarisation	40.8 ± 9.7	43.5 ± 9.4	37.9 ± 9.6
		TMS	41.5 ± 10.3	43.6 ± 10.1	39.2 ± 10.5
		PNS	41.6 ± 11.1	44.6 ± 10.5	38.4 ± 11.2
		$ICC_{3,1}$ (95% CI)	0.94 (0.90 - 0.97)	0.91 (0.81 - 0.97)	0.97 (0.93 - 0.99)
		CV (%)	5.1 ± 2.9	5.8 ± 3.2	4.5 ± 2.6
	Lengthening	Familiarisation	53.4 ± 12.8	55.6 ± 11.9	51.0 ± 13.7
		TMS	54.8 ± 13.6	57.4 ± 13.6	52.0 ± 13.4
		PNS	54.6 ± 14.5	57.7 ± 14.8	51.3 ± 13.9
		$ICC_{3,1}$ (95% CI)	0.94 (0.73 - 0.91)	0.90 (0.79 - 0.96)	0.97 (0.94 - 0.99)
		CV (%)	5.2 ± 3.0	6.3 ± 3.5	4.1 ± 1.9
M_{max} *Amplitude (mV)*	10% isometric MVC	Familiarisation	5.5 ± 2.0	5.7 ± 2.2	5.2 ± 1.9
		TMS	5.8 ± 1.8	6.0 ± 1.7	5.4 ± 1.9
		PNS	5.7 ± 1.8	6.2 ± 1.9	5.4 ± 1.7
		$ICC_{3,1}$ (95% CI)	0.84 (0.73 - 0.91)	0.83 (0.66 - 0.93)	0.85 (0.67 - 0.94)
		CV (%)	13.0 ± 8.2	13.4 ± 9.6	12.7 ± 6.7
	25% isometric MVC	Familiarisation	5.8 ± 2.0	6.2 ± 2.0	5.4 ± 1.9
		TMS	6.0 ± 1.8	6.4 ± 1.9	5.7 ± 1.8
		PNS	6.2 ± 1.7	6.6 ± 1.7	5.8 ± 1.8
		$ICC_{3,1}$ (95% CI)	0.89 (0.80 - 0.94)	0.91 (0.80 - 0.97)	0.86 (0.70 - 0.95)
		CV (%)	10.4 ± 6.8	9.3 ± 6.2	11.5 ± 7.5
	50% isometric MVC	Familiarisation	6.0 ± 1.9	6.3 ± 1.8	5.7 ± 2.0
		TMS	6.5 ± 1.8	6.6 ± 1.9	6.1 ± 1.7
		PNS	6.4 ± 1.7	6.6 ± 1.8	6.3 ± 1.8
		$ICC_{3,1}$ (95% CI)	0.89 (0.82 - 0.95)	0.93 (0.84 - 0.97)	0.87 (0.72 - 0.95)
		CV (%)	8.4 ± 6.3	6.8 ± 4.4	10.1 ± 7.6

Table 2. Effect of contraction type (ISO – isometric, SHO – shortening and LEN – lengthening), intensity (25% and 50% of contraction type specific maximum) and age on voluntary torque, dorsiflexor EMG activity normalised to maximal muscle response (TA RMS) and EMG activity of the antagonist (SOL RMS), responses to percutaneous nerve stimulation (PNS; top half of table) and responses to transcranial magnetic stimulation (TMS; bottom half of table).

		25%			50%		
		ISO	SHO	LEN	ISO	SHO	LEN
CV_{torque} (%)	Young	1.8 ± 1.1‡	4.7 ± 1.8	4.3 ± 1.6	1.5 ± 0.5‡	4.7 ± 1.1	4.1 ± 1.0
	Older	2.2 ± 1.6‡	9.1 ± 2.3*#	7.7 ± 3.1*	1.7 ± 0.6‡	9.3 ± 2.4*#	8.6 ± 7.4*
Torque (% MVC)	Young	25.0 ± 0.7	24.6 ± 1.4	28.3 ± 2.7§	49.5 ± 1.0	48.0 ± 4.0	50.9 ± 7.0
	Older	25.2 ± 1.1	24.0 ± 2.0	30.4 ± 3.2§	49.6 ± 1.0	47.3 ± 2.3§	53.2 ± 3.9§
TA RMS (/ M_{max})	Young	0.014 ± 0.004	0.018 ± 0.005†	0.013 ± 0.003	0.024 ± 0.004	0.031 ± 0.006†	0.025 ± 0.008
	Older*	0.018 ± 0.005‡	0.025 ± 0.006	0.023 ± 0.008	0.029 ± 0.007‡	0.038 ± 0.011	0.035 ± 0.010
SOL RMS (mV)	Young	0.007 ± 0.001	0.009 ± 0.002$	0.008 ± 0.002	0.012 ± 0.003	0.015 ± 0.004$	0.012 ± 0.003
	Older	0.008 ± 0.002	0.010 ± 0.002$	0.010 ± 0.003$	0.011 ± 0.003	0.014 ± 0.004$	0.015 ± 0.004$
H latency (ms)	Young	33.4 ± 1.9	33.5 ± 1.8	33.4 ± 2.3	33.4 ± 1.6	33.1 ± 1.7	33.3 ± 2.2
	Older	35.0 ± 3.4	35.7 ± 3.3	34.9 ± 3.7	34.9 ± 3.7	36.1 ± 3.8	35.4 ± 3.5
M_H/M_{max}	Young	0.19 ± 0.02	0.18 ± 0.03	0.17 ± 0.02	0.19 ± 0.03	0.18 ± 0.05	0.18 ± 0.02
	Older	0.18 ± 0.01	0.17 ± 0.02	0.15 ± 0.05	0.18 ± 0.01	0.19 ± 0.02	0.18 ± 0.02
CV_{torque} (%)	Young	1.6 ± 0.5‡	4.8 ± 1.2	4.3 ± 1.3	1.3 ± 0.4‡	5.0 ± 1.0	3.7 ± 0.7
	Older	2.2 ± 1.2‡	11.1 ± 3.4*#	7.7 ± 3.7*	1.7 ± 0.7‡	9.2 ± 5.1*#	6.1 ± 3.3*
Torque (% MVC)	Young	25.1 ± 1.0	24.4 ± 1.9	28.1 ± 2.8§	49.7 ± 0.9	49.9 ± 3.2	46.6 ± 3.4§
	Older	25.1 ± 1.1	23.9 ± 2.0	30.2 ± 2.2§	49.5 ± 1.6	53.3 ± 2.9§	52.4 ± 3.1§
TA RMS (/ M_{max})	Young	0.013 ± 0.004	0.017 ± 0.005†	0.013 ± 0.003	0.024 ± 0.006	0.028 ± 0.007†	0.025 ± 0.006
	Older*	0.019 ± 0.006‡	0.027 ± 0.015	0.026 ± 0.012	0.030 ± 0.011‡	0.033 ± 0.011	0.034 ± 0.013
SOL RMS (mV)	Young	0.007 ± 0.001	0.009 ± 0.003$	0.007 ± 0.002	0.012 ± 0.004	0.014 ± 0.005$	0.013 ± 0.003
	Older	0.007 ± 0.003	0.009 ± 0.003$	0.010 ± 0.003$	0.011 ± 0.004	0.013 ± 0.004$	0.014 ± 0.005$
MEP latency (ms)	Young	29.9 ± 3.5	29.7 ± 2.3	29.1 ± 3.1	29.5 ± 4.3	28.6 ± 2.8	28.5 ± 4.3
	Older*	34.2 ± 7.9	33.4 ± 5.8	35.7 ± 7.5	31.8 ± 5.0	33.5 ± 7.3	33.1 ± 6.2

M_H/M_{max} = M-wave when H-reflex was evoked normalised to maximal muscle response; RMS = root-mean-square EMG activity.

Torque, TA RMS and SOL RMS increased with contraction intensity.

$p < 0.05$ - *compared to younger; † compared to ISO and ECC; ‡ compared to CON and ECC; #compared to ECC; §compared to target %; $compared to ISO

Figure captions

Figure 1. Tibialis anterior fascicle length (mm) with changes in the ankle joint angle during shortening (left panel) and lengthening (centre panel), and isometric (right panel) contractions at 50% of contraction type specific MVC. Fascicle length was assessed every 5º throughout the range-of-motion for shortening and lengthening contractions and are displayed on the x-axes relative to anatomical zero (ankle at 90º). Fascicles changed linearly with changes in joint angle as noted on plots. For isometric contractions, fascicle length was assessed every second of the contraction, corresponding to the timing of every 5º-change during the dynamic contractions. Full lines represent the sample mean, whilst dashed lines denote individual responses.

Figure 2. Maximum voluntary contraction torque during different contraction types (ISO – isometric, SHO – shortening, LEN – lengthening; A and B), maximal compound action potential amplitude (C and D) and maximal compound action potential latencies at different contraction intensities (E and F) in young (left panel) and older (right panel) individuals. Open circles denote individual response and open squares denote the age group mean.

Figure 3. Responses to percutaneous nerve stimulation. A: Representative examples from one young (black line) and older (grey line) individual during isometric, shortening and lengthening contraction at 25% of contraction type specific MVC. The downward arrows denote the point of stimulation and the dotted circles indicate the H-reflex. Both participants were of similar height. All traces are an average of 4 waveforms. B–E: The amplitude of H-reflex normalised to maximal muscle response (H/M_{max}) in young (left panel) and older (right panel) adults at 25% (B, C) and 50% (D, E) maximal torque during isometric (ISO), shortening (SHO) and lengthening (LEN) contractions. Open circles denote individual response and open squares denote the age group mean.

Figure 4. Responses to TMS. A: Representative examples from one young (black line) and older (grey line) individual during isometric, shortening and lengthening contraction at 25% of contraction type specific MVC. Each trace begins at the stimulus artefact and shows 150 milliseconds. The vertical dashed lines represent the onset of MEP (latency). Both participants were of similar height. All traces are an average of 4 waveforms. B–E: The amplitude of motor evoked potential normalised to maximal muscle response (MEP/M_{max}) in young (left panel) and older (right panel) adults at 25% (B, C) and 50% (D, E) maximal torque during isometric (ISO), shortening (SHO) and lengthening (SHO) contractions. Open circles denote individual response and open squares denote the age group mean.

Figure 5. Evoked responses normalised to pre-stimulus root-mean-square EMG activity ($[H/M_{max}]/RMS$, A–D; and $[MEP/M_{max}]/RMS$, E–G) in young (left panel) and older (right panel) adults at 25% and 50% of maximal torque during isometric (ISO), shortening (SHO) and lengthening (LEN) contractions. Open circles denote individual response and open squares denote the age group mean. $^{\#}p < 0.010$ compared to ISO and CON.

Additional information

Author contributions

J.Š., G.H., S.G. and R.D. conceived and designed research; J.Š., P.A., C.G.B. and K.M.H. performed experiments; J.Š. analysed data; J.Š. and R.D. interpreted results; J.Š. prepared figures and drafted manuscript; all authors edited and revised manuscript; all authors approved final version of manuscript.

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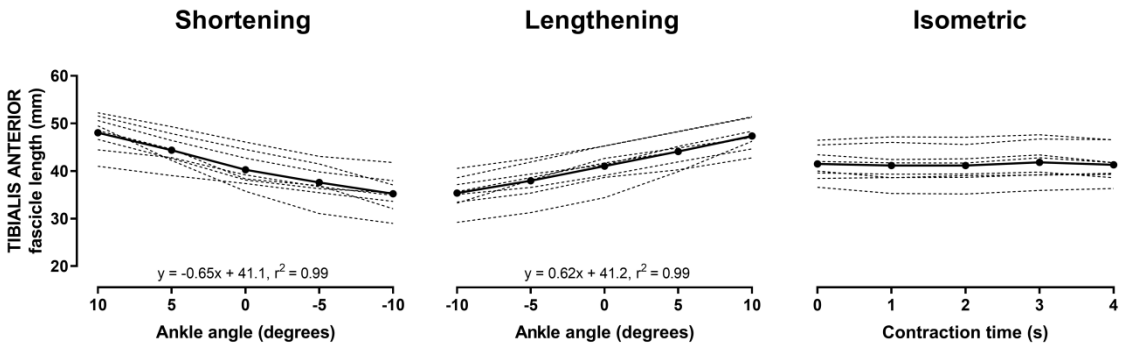
Disclosures

The authors declare no conflict of interest, financial or otherwise.

1168 Figure 1



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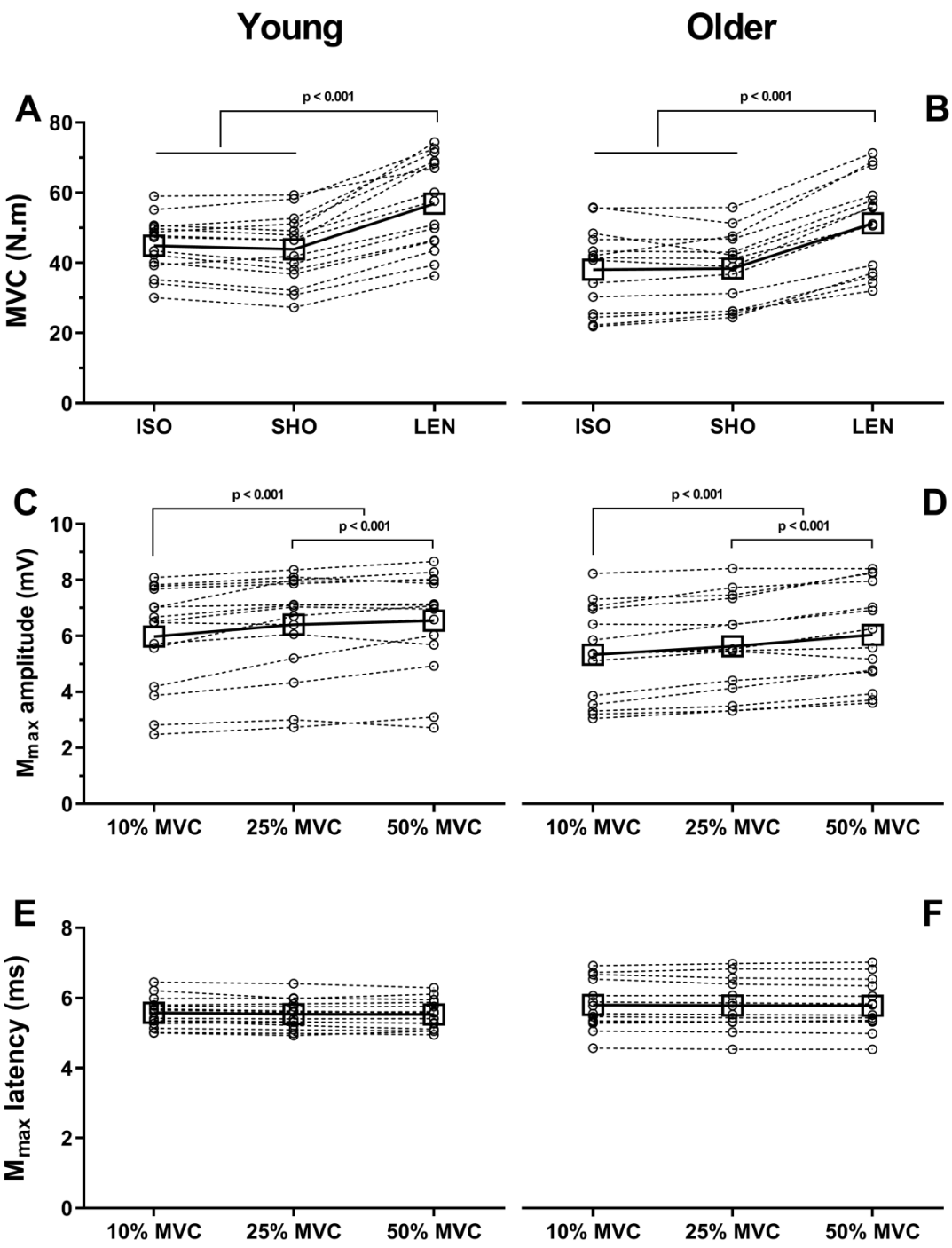
1171 Figure 2



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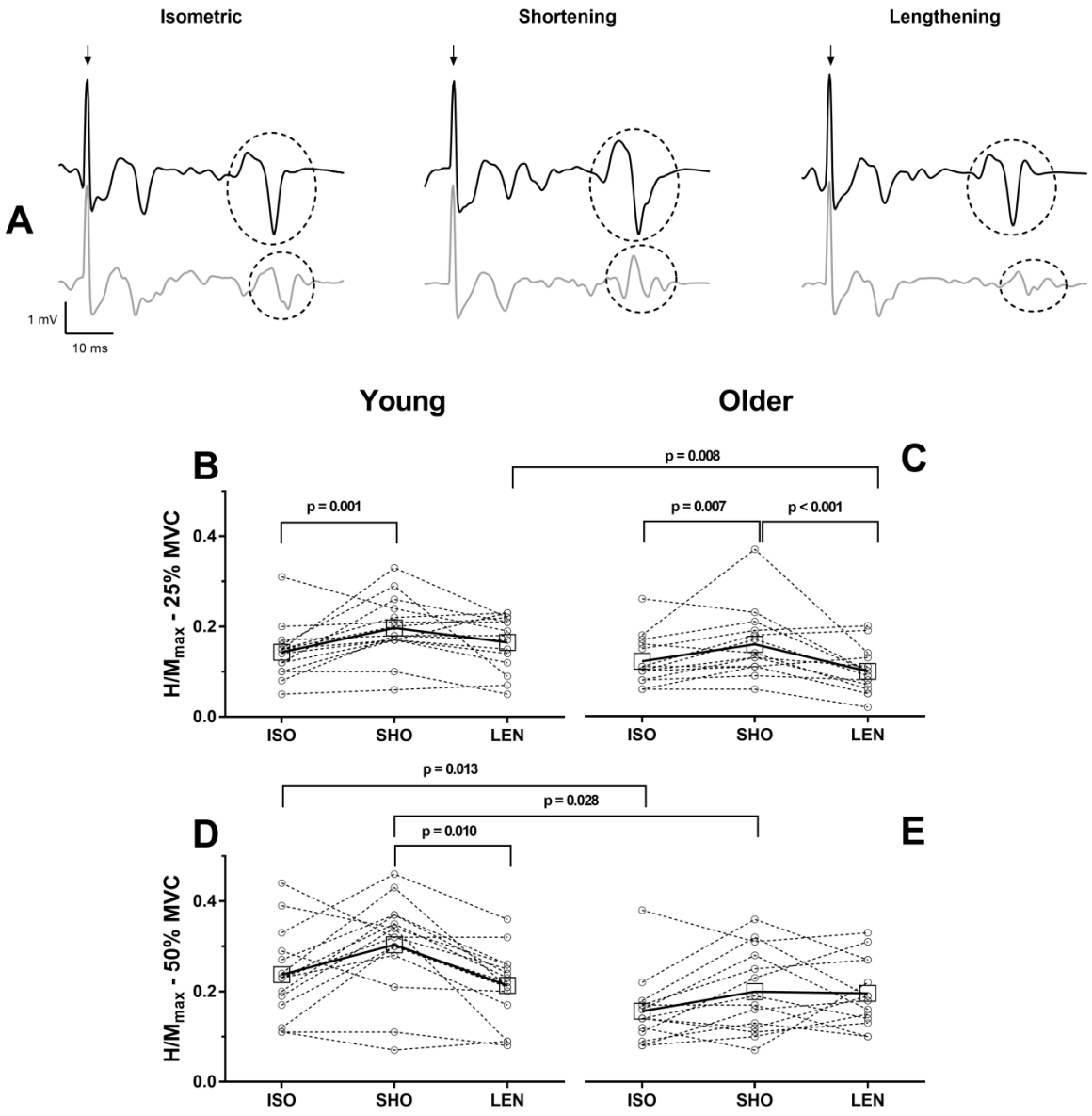
1174 Figure 3



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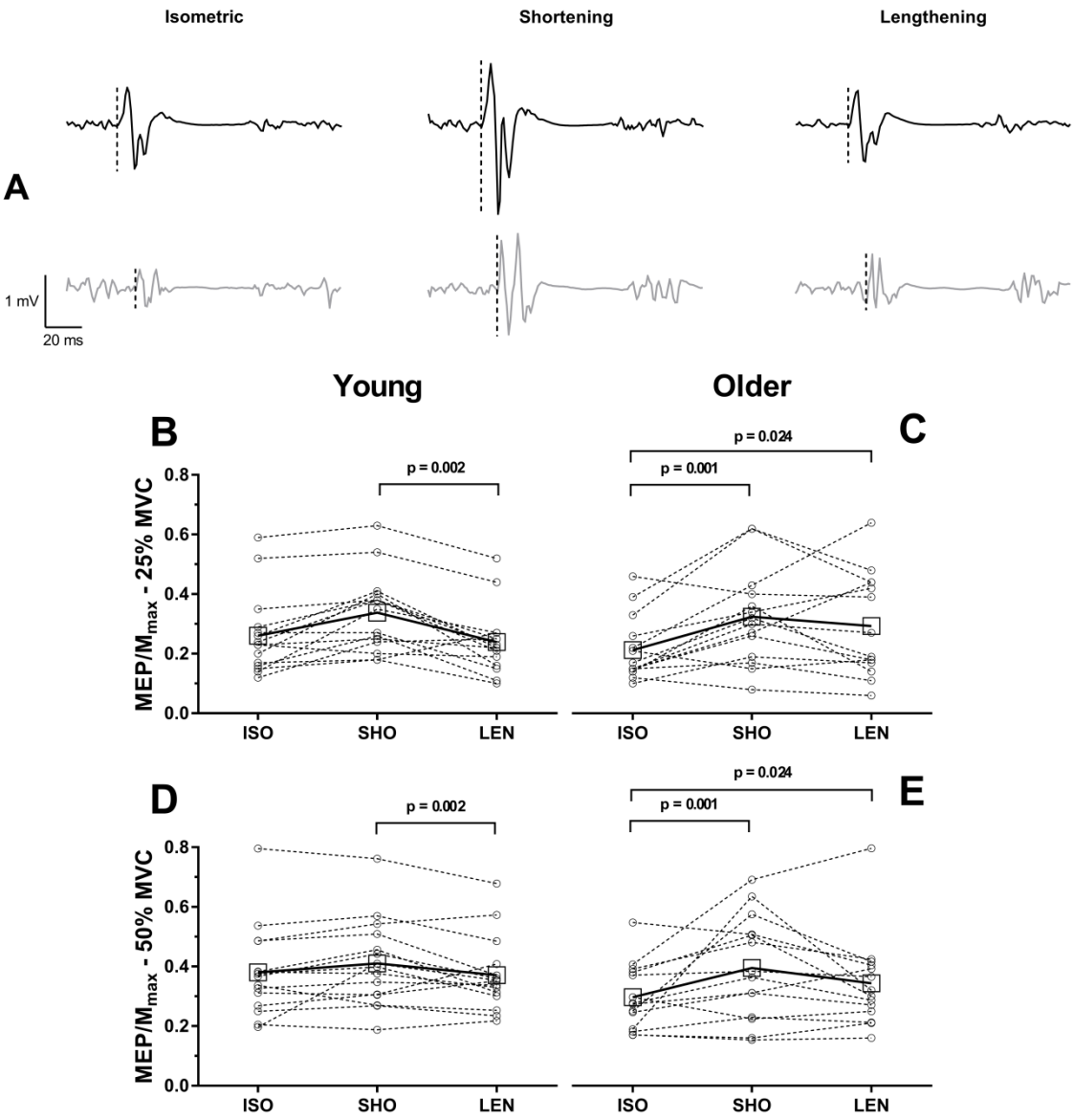

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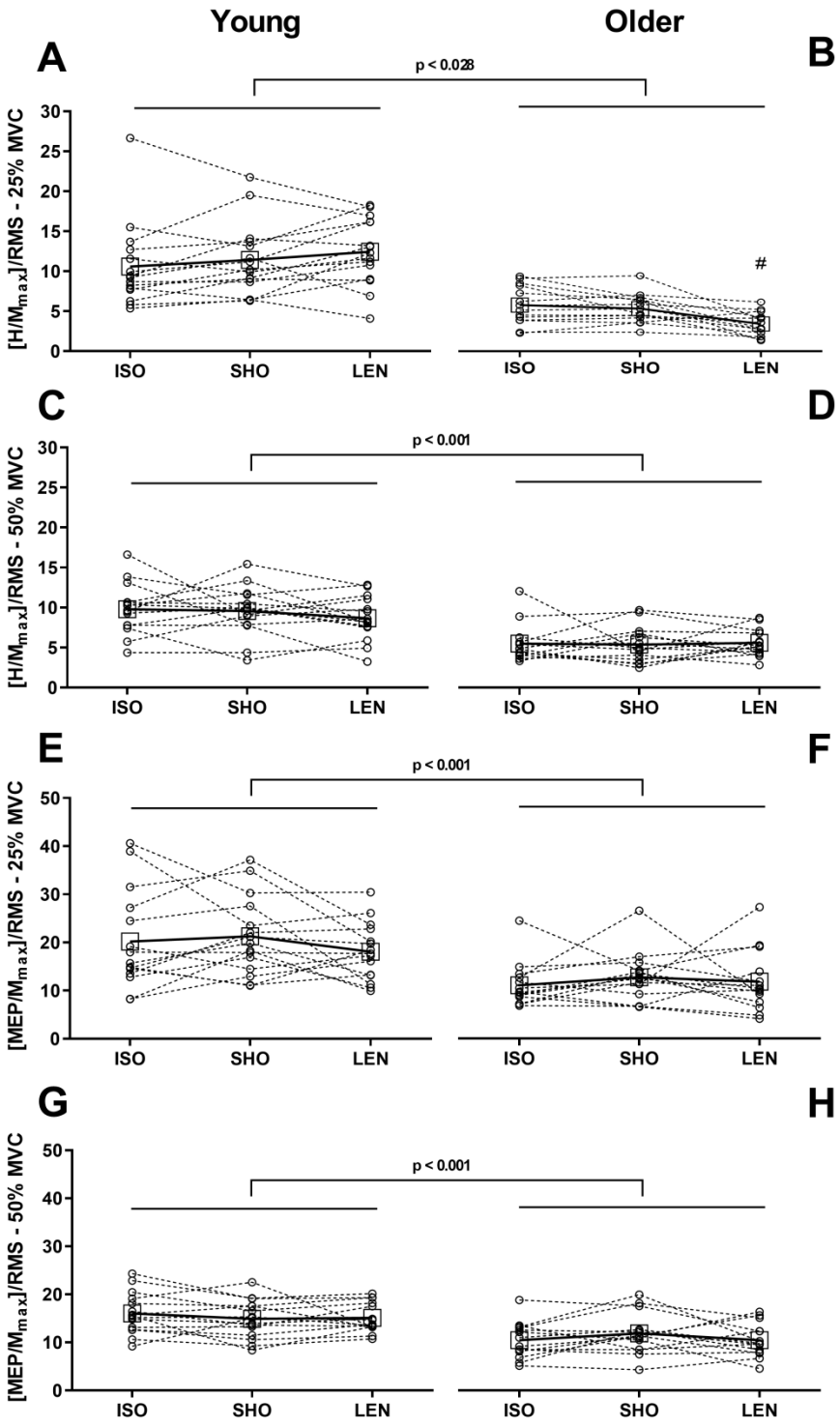
1179 Figure 5



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